Group movement ‘initiation’ and state-dependent decision-making

Sean A. Rands

Centre for Behavioural Biology, School of Veterinary Science,
University of Bristol, Langford, Bristol BS40 5DU, UK
tel +44 117 331 9038

email sean.rands@bristol.ac.uk

*NOTICE: this is the author’s version of a work that was accepted for publication in **Behavioural Processes**. Changes resulting from the publishing process, such as peer review, editing, corrections, structural formatting, and other quality control mechanisms may not be reflected in this document. Changes may have been made to this work since it was submitted for publication. A definitive version was subsequently published in*
Behavioural Processes 84(3): 668-670 doi: 10.1016/j.beproc.2010.03.001

Groups don't necessarily need leaders to show coherence in their behaviour (Camazine et al. 2001, Couzin and Krause 2003). However, as **Petit and Bon (THIS ISSUE)** describe, collective behaviours may often be initiated by one or a few individuals, and much recent work has considered the role of leaders and decision-makers in this process (King and Cowlishaw 2009, King et al. 2009). Whether the decision about where and when the group of animals should move is made by one or many of the group members, this decision ultimately has to be mirrored by the other members of the group. Therefore, picking apart the processes involved in this pre-movement phase is important for us to be able to understand collective group movements.

If the decision to move is spread among more than one member of the group, we could assume that either there is some democratic process involved in making the decision (Conradt and List 2009), or else the group-level behaviour is an emergent property of the combined individual decisions of the members of the group (Camazine et al. 2001, Couzin and Krause 2003). Note that, in the former case, group decisions are made by multiple individuals coming to a joint decision which is then followed by the group, whilst in the latter, the 'decision' of the group emerges as a consequence of the combined actions of the individuals, and doesn't require any of the group's members to actively make decisions about how the group should be behaving as a whole. In proposed cases of the former, the true test of whether decision-making is spread through the group would be to first identify the mechanism of the 'democratic' process, and then experimentally manipulate it (in order to demonstrate that it is indeed the mechanism). The many observational studies of various species outlined by **Petit and Bon (THIS ISSUE)** go some of the way to the first of these steps, but I would argue that we need to make much more headway in identifying the mechanisms behind collective decision-making, and testing them with experimental manipulations, before we can conclusively say that we are observing genuine collective decision-making leading to co-ordinated movements. For example, discussion of group 'voting' behaviour frequently dwells on the pre-movement 'initiator' behaviours such as those shown by female African buffalo, *Syncerus caffer* (Prins 1996), where individuals are recorded as standing and pointing in the 'intended' movement direction of the group in the extended period before the group moves, where the ultimate movement correlates with some measure of the average direction pointed towards in the pre-movement period. This is a nice example if it is true, but all we see here is a strong correlation between the group's ultimate direction of movement, and one particular activity seen before that movement takes place. But correlation between consecutive actions does not prove that the first action has any effect upon the second action occurring – there is nothing to demonstrate that pointing has any influence on the behaviour of the group, which is why we need to conduct experimental manipulations to demonstrate that the 'intention' behaviour indeed initiates the collective group movement. Many studies report a correlation between pre-movement behaviours and actual movement (Kummer 1968, Dumont et al. 2005, Bourjade et al. 2009, Ramseyer et al. 2009a, b, c, Sueur and Petit in press), and a similar need for experimental testing is required to demonstrate that the ‘intention’ behaviours of one or many individuals are anything other than activities that show a correlation with movement.

However, even a thorough combination of observational and experimental manipulations isn’t enough to gain a complete understanding of the function and mechanisms behind collective behaviours: a solid theoretical framework is also necessary. Agent-based models can be used to demonstrate various forms of group-level movement that can occur when different individuals have different interests or properties (Rands et al. 2006, Dyer et al. 2008, Ward et al. 2008, Conradt et al. 2009), but ultimately, to understand the mechanisms behind these movements, we need to understand the function of these mechanisms from an evolutionary perspective. Because multiple individuals who may have differing and potentially conflicting interests are involved in the movements, this framework needs to consider evolutionary games that could be played out between the members of the group, which in turn means that we need to understand the costs that the different actions available to each member of a group have upon their fitnesses.

The state-dependent approach to behaviour (Houston and McNamara 1999, Clark and Mangel 2000) offers a means of making evolutionarily-grounded predictions about behavioural rules based upon some simple assumptions about the link between an animal’s actions and their effects upon the animal’s fitness. Any behaviour conducted by the animal will change important aspects of itself – for example, its energy reserves, or number of offspring – which, when combined, are referred to as the animal’s *state*. State-dependent techniques allow us to link different measures of state at particular moments in time or an individual’s life history with corresponding measures of fitness. This means that it is possible to predict optimal sequences of behaviour, given that conducting particular actions will lead to a definable change in the animal’s state. For example, the foraging decisions over the course of a winter’s day that are made by small birds have been well characterised (Houston and McNamara 1993, McNamara et al. 1994, Brodin 2007). In these models, foraging is a dangerous activity that exposes the bird to predators, but resting (thus avoiding foraging) means that the bird is using vital energy, and it has to build up sufficient reserves to survive through the night (when it is unable to forage) as well as counteract unexpected bad environmental conditions. If the state of the bird is characterised by its energy reserves, foraging will, on average, lead to an increase in state, whilst resting leads to a decrease. The bird therefore faces a trade-off between starvation and predation through its choice of behaviour (McNamara and Houston 1990, Houston et al. 1993): low energy reserves increase the chances of starvation, whilst high energy reserves mean an increase in predation (both through the increased amount of foraging required to maintain them, as well as possible physiological effects on escape ability – Witter and Cuthill 1993), and the fitness value of being at a particular state level is going to change through the course of the day. This example shows that, by using state-dependent modelling techniques, the effects of multiple factors (in this case, physiological effects and predation risk) can be considered together using the unifying currency of fitness, and it should be noted that these techniques can allow us to make predictions about moment-to-moment behaviour at very fine time-scales, provided that the set of behaviours that are available to an individual (or group of individuals) lead to different changes in whichever aspect of each individual's state is being measured. Observational and manipulative experiments have demonstrated that these models produce extremely robust predictions about foraging routines (Rands and Cuthill 2001), demonstrating that state-dependent models are able to generate qualitatively tractable predictions (Hutchinson and McNamara 2000), which are often experimentally testable if we are able to compare measures of state relevant to the modelling process (such as levels of fat reserves) in response to differing environmental conditions or, most ideally, if we are able to manipulate the environment appropriately (such as by food supplementation, or altering perceived predation risk). Hutchinson and McNamara (2000) discuss in great detail what can and cannot be tested when we attempt to combine state-dependent modelling techniques with field observations.

Any economic consideration of the behaviour of multiple individuals who have potential conflicts of interest is likely to involve game theory, and techniques exist for modelling state-dependent decision-making processes using a game theoretic approach (Houston and McNamara 1999). A series of game theory models have been developed that explore social foraging behaviour from a state-dependent perspective (Rands et al. 2003, Rands and Johnstone 2006, Rands et al. 2008). These models consider a pair of animals, where each individual can choose to either rest or forage during a short period of time. As with the 'small bird in winter' model described above, the energy reserves of each of the individual animals is considered as its state, and the action taken by an individual can, on average, lead to energy reserves increasing (when foraging) or decreasing (when resting). However, the combined actions of the pair of animals also has an effect, and synchronising actions can affect the likelihood of predation experienced by both individuals: an individual is less likely to be predated when its foraging is synchronised with its colleague, compared to when it is foraging alone. These models demonstrate that if individuals are able to assess both their own state (which they should know) and the state of their co-forager (which they should be able to assess to some degree of accuracy), then the behaviour of both of the animals should become highly synchronised, where the individual with the lower energy reserves (or greatest energetic needs) is the individual determining whether the pair are foraging or resting during a period of time. The rule-sets generated by these models give a robust set of predictions about how the short-term behaviour of the members of a group can be a direct result of the information they have about the state of themselves and the other group members, based on an understanding of the functional explanation for the behaviours.

Activity synchronisation is seen in many species (reviewed by Rands et al. 2008), and these results could be extended to consider the synchronised decisions made to start and continue collective movements of groups, where 'initiation' movements could give a reliable indication of the state of a group member (regardless of whether the initiating activity itself is the cause of the collective behaviour, or simply a by-product behaviour of some other feature of the individual's state that can be separately assessed by other group members). Experimental evidence from systems similar to these state-dependent model suggest that there is a link between differences in energetic state and initiation behaviour (de Laet 1985, Black 1988, Hogstad 1988, Gotceitas and Godin 1991, Fischhoff et al. 2007; but see Stueckle and Zinner 2008, Šárová et al. 2007). However, it is computationally difficult to explore the state-dependent decision-making processes of large groups of animals, which is why, to present, the models described above only calculate the optimal rule-sets for a pair of foraging individuals. Rands et al. (2004, 2006) suggest an intermediate approach to address this problem, by mixing the evolutionarily-sound rules derived for pairs of animals with some likely candidates for how these rules could be extended for larger groups, using an agent-based approach. However, although the technique is ideal for exploring group-movement initiation behaviours shown by individuals, this wasn't quantified within these papers, and there is potential for some interesting exploration of movement initiation from a functional perspective using these techniques.

Therefore, using a state-dependent perspective is essential for a clear, evolutionarily-grounded understanding of how and when collective group behaviours are initiated and conducted. A mixture of these techniques with agent-based simulations and with careful experimental manipulations should give us many new insights into this intriguing social behaviour.

Black, J.M., 1988. Preflight signalling in swans: a mechanism for group cohesion and flock formation. Ethology, 79: 143-157. (d.o.i.

Bourjade, M., Thierry, B., Maumy, M. and Petit, O., 2009. Decision-making in Przewalski horses (*Equus ferus przewalskii*) is driven by the ecological contexts of collective movements. Ethology, 115: 321-330. (d.o.i. 10.1111/j.1439-0310.2009.01614.x)

Brodin, A., 2007. Theoretical models of adaptive energy management in small wintering birds. Phil. Trans. R. Soc. B, 362: 1857-1871. (d.o.i. 10.1098/rstb.2006.1812)

Camazine, S., Deneubourg, J.-L., Franks, N.R., Sneyd, J., Theraulaz, G. and Bonabeau, E., 2001. Self-organization in biological systems. Princeton University Press, Princeton, 560 pp.

Clark, C.W. and Mangel, M., 2000. Dynamic state variable models in ecology: methods and applications. Oxford University Press, New York, 289 pp.

Conradt, L., Krause, J., Couzin, I.D. and Roper, T.J., 2009. "Leading according to need" in self-organizing groups. Am. Nat., 173: 304-312. (d.o.i. 10.1086/596532)

Conradt, L. and List, C., 2009. Group decisions in humans and animals: a survey. Phil. Trans. R. Soc. B, 364: 719-742. (d.o.i. 10.1098/rstb.2008.0276)

Couzin, I.D. and Krause, J., 2003. Self-organization and collective behavior in vertebrates. Adv. Stud. Behav., 32: 1-75. (d.o.i. 10.1016/S0065-3454(03)01001-5)

de Laet, J.F., 1985. Dominance and anti-predator behaviour of great tits *Parus major*: a field study. Ibis, 127: 372-377.

Dumont, B., Boissy, A., Achard, C., Sibbald, A.M. and Erhard, H.W., 2005. Consistence of animal order in spontaneous group movements allows the measurement of leadership in a group of grazing heifers. Appl. Anim. Behav. Sci., 95: 55-66. (d.o.i. 10.1016/j.applanim.2005.04.005)

Dyer, J.R.G., Ioannou, C.C., Morrell, L.J., Croft, D.P., Couzin, I.D., Waters, D.A. and Krause, J., 2008. Consensus decision making in human crowds. Anim. Behav., 75: 461-470. (d.o.i. 10.1016/j.anbehav.2007.05.010)

Fischhoff, I.R., Sundaresan, S.R., Cordingley, J., Larkin, H.M., Sellier, M.-J. and Rubenstein, D.I., 2007. Social relationships and reproductive state influence leadership roles in movements of plains zebra, *Equus burchellii*. Anim. Behav., 73: 825-831. (d.o.i. 10.1016/j.anbehav.2006.10.012)

Gotceitas, V. and Godin, J.-G.J., 1991. Foraging under the risk of predation in juvenile Atlantic salmon (*Salmo salar* L.): effects of social status and hunger. Behav. Ecol. Sociobiol., 29: 255-261. (d.o.i. 10.1007/BF00163982)

Hogstad, O., 1988. Social rank and antipredator behaviour of willow tits *Parus montanus* in winter flocks. Ibis, 130: 45-56.

Houston, A.I. and McNamara, J.M., 1993. A theoretical investigation of the fat reserves and mortality levels of small birds in winter. Ornis Scand., 24: 205-219.

Houston, A.I. and McNamara, J.M., 1999. Models of adaptive behaviour: an approach based on state. Cambridge University Press, Cambridge, 378 pp.

Houston, A.I., McNamara, J.M. and Hutchinson, J.M.C., 1993. General results concerning the trade-off between gaining energy and avoiding predation. Phil. Trans. R. Soc. Lond. B, 341: 375-397. (d.o.i. 10.1098/rstb.1993.0123)

Hutchinson, J.M.C. and McNamara, J.M., 2000. Ways to test stochastic dynamic programming models empirically. Anim. Behav., 59: 665-676. (d.o.i. 10.1006/anbe.1999.1362)

King, A.J. and Cowlishaw, G., 2009. Leaders, followers, and group decision-making. Commun. Integr. Biol., 2: 147-150.

King, A.J., Johnson, D.D.P. and Van Vugt, M., 2009. The origins and evolution of leadership. Curr. Biol., 19: R911-R916. (d.o.i. 10.1016/j.cub.2009.07.027)

Kummer, H., 1968. Social organisation of hamadryas baboons: a field study. Karger, Basel, 189 pp.

McNamara, J.M. and Houston, A.I., 1990. The value of fat reserves and the tradeoff between starvation and predation. Acta Biotheor., 38: 37-61. (d.o.i. 10.1007/BF00047272)

McNamara, J.M., Houston, A.I. and Lima, S.L., 1994. Foraging routines of small birds in winter: a theoretical investigation. J. Avian Biol., 25: 287-302.

PETIT & BON CITATION (TARGET REVIEW IN THIS ISSUE)

Prins, H.H.T., 1996. Ecology and behaviour of the African buffalo. Chapman & Hall, London, 320 pp.

Ramseyer, A., Boissy, A., Dumont, B. and Thierry, B., 2009a. Decision making in group departures of sheep is a continuous process. Anim. Behav., 78: 71-78. (d.o.i. 10.1016/j.anbehav.2009.03.017)

Ramseyer, A., Petit, O. and Thierry, B., 2009b. Decision-making in group departures of female domestic geese. Behaviour, 146: 351-371. (d.o.i. 10.1163/156853909X410955)

Ramseyer, A., Thierry, B., Boissy, A. and Dumont, B., 2009c. Decision-making processes in group departures of cattle. Ethology, 115: 948-957. (d.o.i. 10.1111/j.1439-0310.2009.01686.x)

Rands, S.A., Cowlishaw, G., Pettifor, R.A., Rowcliffe, J.M. and Johnstone, R.A., 2003. The spontaneous emergence of leaders and followers in a foraging pair. Nature, 423: 432-434. (d.o.i. 10.1038/nature01630)

Rands, S.A., Cowlishaw, G., Pettifor, R.A., Rowcliffe, J.M. and Johnstone, R.A., 2008. The emergence of leaders and followers in foraging pairs when the qualities of individuals differ. BMC Evol. Biol., 8: 51. (d.o.i. 10.1186/1471-2148-8-51)

Rands, S.A. and Cuthill, I.C., 2001. Separating the effects of predation risk and interrupted foraging upon mass changes in the blue tit *Parus caeruleus*. Proc. R. Soc. B, 268: 1783-1790. (d.o.i. 10.1098/rspb.2001.1653)

Rands, S.A. and Johnstone, R.A., 2006. Statistical measures for defining an individual's degree of independence within state-dependent dynamic games. BMC Evol. Biol., 6: 81. (d.o.i. 10.1186/1471-2148-6-81)

Rands, S.A., Pettifor, R.A., Rowcliffe, J.M. and Cowlishaw, G., 2004. State-dependent foraging rules for social animals in selfish herds. Proc. R. Soc. B, 271: 2613-2620. (d.o.i. 10.1098/rspb.2004.2906)

Rands, S.A., Pettifor, R.A., Rowcliffe, J.M. and Cowlishaw, G., 2006. Social foraging and dominance relationships: the effects of socially mediated interference. Behav. Ecol. Sociobiol., 60: 572-581. (d.o.i. 10.1007/s00265-006-0202-4)

Šárová, R., Špinka, M. and Panamá, J.L.A., 2007. Synchronization and leadership in switches between resting and activity in a beef cattle herd – a case study. Appl. Anim. Behav. Sci., 108: 327-331. (d.o.i. 10.1016/j.applanim.2007.01.009)

Stueckle, S. and Zinner, D., 2008. To follow or not to follow: decision making and leadership during the morning departure in chacma baboons. Anim. Behav., 75: 1995-2004. (d.o.i. 10.1016/j.anbehav.2007.12.012)

Sueur, C. and Petit, O., in press. Signals use by leaders in *macaca tonkeana* and *Macaca mulatta*: group-mate recruitment and behaviour monitoring. Anim. Cognit. (d.o.i. 10.1007/s10071-009-0261-9)

Ward, A.J.W., Sumpter, D.J.T., Couzin, I.D., Hart, P.J.B. and Krause, J., 2008. Quorum decision-making facilitates information transfer in fish shoals. Proc. Natl. Acad. Sci. USA, 105: 6948-6953. (d.o.i. 10.1073/pnas.0710344105)

Witter, M.S. and Cuthill, I.C., 1993. The ecological costs of avian fat storage. Phil. Trans. R. Soc. Lond. B, 340: 73-92. (d.o.i. 10.1098/rstb.1993.0050)